7. On the Mode of Growth and the Structure of the Shell in *Velates conoideus*, Lamk., and other *Neritidæ*. By B. B. Woodward, F.G.S., F.R.M.S. (Communicated by Prof. Flower, C.B., President.)

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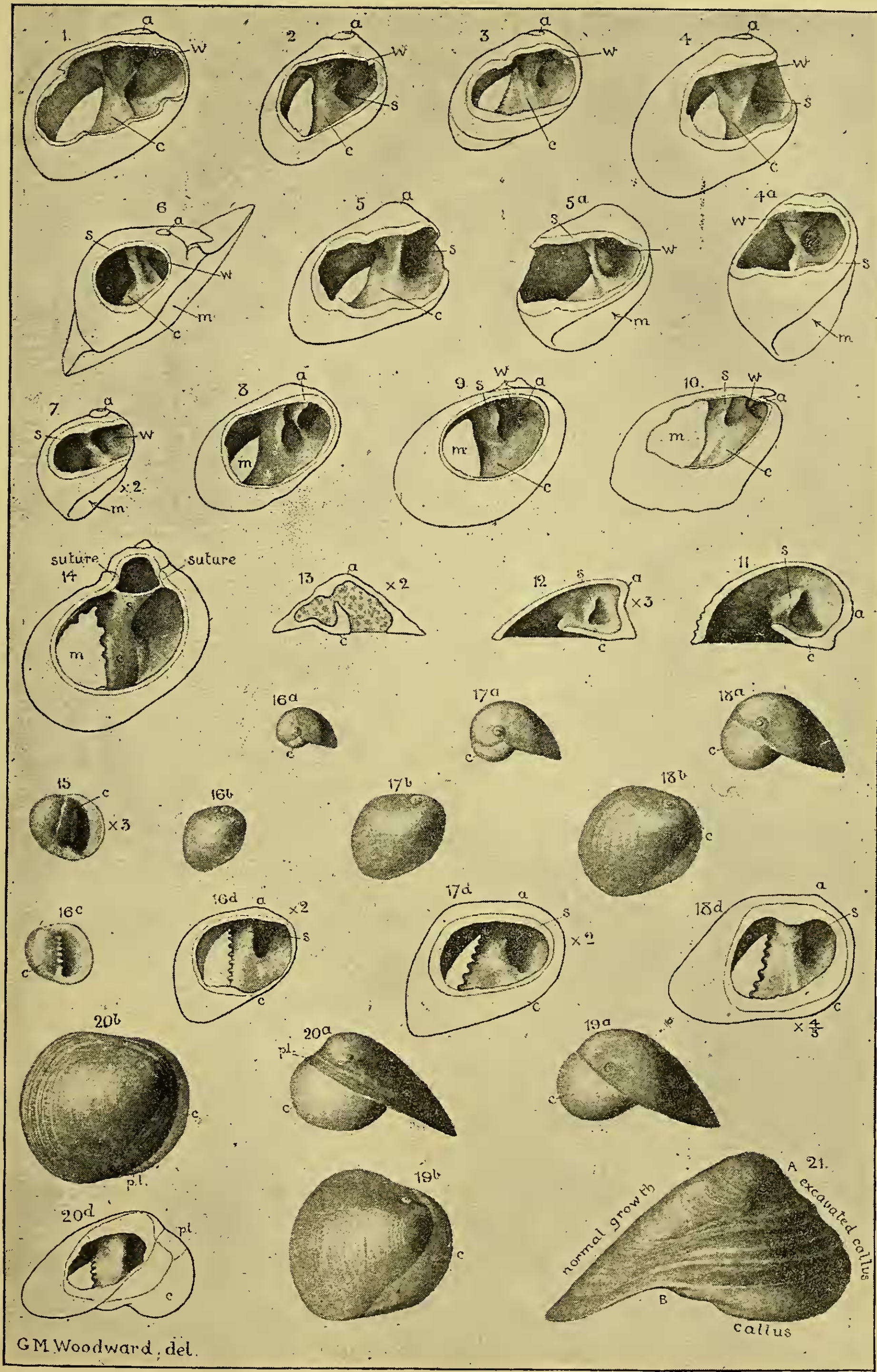
(Plates XXXI. & XXXII.)

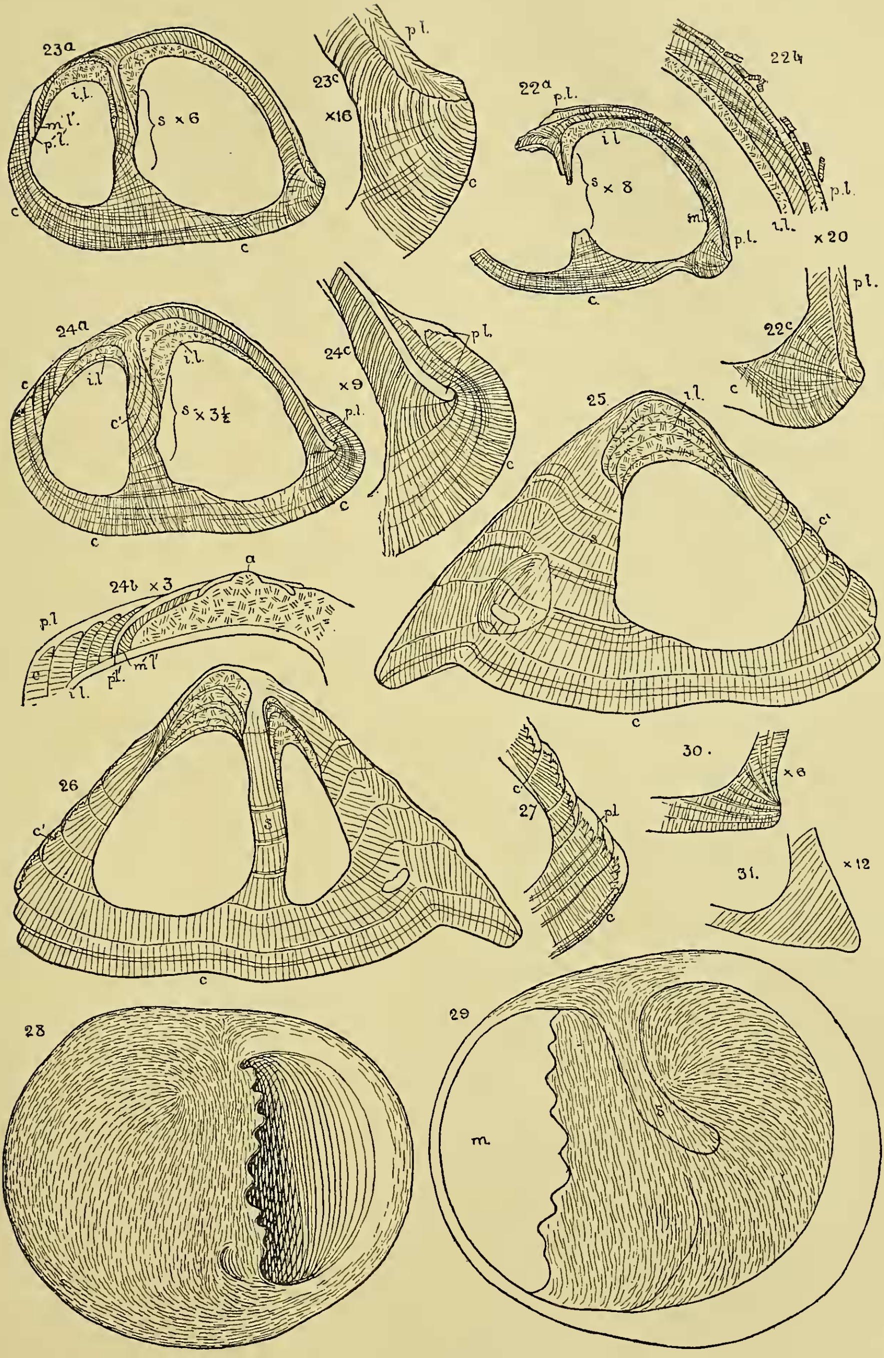
At the June meeting of this Society in 1889 attention was drawn by the writer to the very peculiar method of growth of the shell which forms the principal subject of this communication, as was shown by sections of specimens then exhibited. Unfortunately a far too prevalent epidemic interfered for the time with further investigation, which on being resumed has lead to more extended inquiry than at first contemplated, with results, however, which it is hoped may prove to be of some interest. The species was then spoken of as *Neritina schmideliana*; but on reference to the literature it appears that this name cannot stand, since Chemnitz's description[1] was published prior to the adoption, in the 'Conchylien-Cabinet,' of the binomial system of nomenclature. The next name in order of priority was that conferred by Gmelin in his edition of Linné's 'Systema Naturæ'[2], where he quotes Chemnitz, and under the impression it was a sinistral species calls it *Nerita perversa*. This, however, is such a complete misnomer that it seems wiser to set it aside, as recommended in such cases by the British Association Rules, and to adopt the specific name of *conoideus* conferred on it by Lamarck[3]. The generic name of *Velates* proposed by Montfort[4] should also be adopted, since, judging from the evidence afforded by its shell, the animal must have differed in important respects from both of its nearest allies—*Nerita* and *Neritina*. Other conchologists have described and figured the shell, notably Deshayes, who also first figured the operculum; but all save Schmidel[5] seem to have confined their attention to its external aspect and to have overlooked its internal arrangement and its remarkable mode of growth after the earlier stages of its existence have passed. Before, however, this can be dealt with it is necessary, in the first instance, to briefly describe certain features in the internal structure of other members of the family to which it belongs.

The Neritidæ, it is well known, avail themselves largely of the molluscan faculty of removing portions of the shell that may be in the way of the animal in the course of its growth, and some of them in this manner convert the interior of their tenement into a single open chamber across which there projects from the side, immediately

[1] Mart. and Chemn. Conch.-Cab. ix. (1786) p. 130.
[2] Linnæus, Syst. Nat., ed. curâ Gmelin (1789), tom. i. p. 3686.
[3] *Nerita conoidea*, Ann. Mus. Paris, v. (1804) p. 93.
[4] Conch. Syst. ii. (1810) pp. 354–6, fig.
[5] A list of the more important references is given at the end of this paper.



STRUCTURE OF NERITINA, VELATES, ETC.



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behind the posterior portion of the columellar lip, a septum that takes the place of the columella and serves as the point of attachment for the posterior retractor muscle. This structural alteration is effected not after the animal has completed growth, but proceeds *pari passu* with it.

In *Neritina* a series of species may be selected which will exhibit stages in the degree of removal of the columella and inner walls of the whorls and in the development of the septum.

Neritina cornea, Linn. (Plate XXXI. fig. 1), *N. gagates*, Lamk. (fig. 2), and thin specimens of *N. zebra*, Linn., and *N. dubia*, Chem., show an early stage. There is no true columella, and some portion of the columella-edge of the spiral party-wall (or *paries*) separating the whorls has been removed. At the base of the columella-edge where the parietal wall joins the projecting columellar lip the angle is filled in with shelly matter strengthening the union between the two. A slight spur of the shelly deposit runs in some cases (*N. gagates* and *N. zebra*) up the columella-edge and supports it. The whole forms a myophore and serves as a point of attachment for the posterior retractor muscle, a slight salient point left in some species about halfway up on the columella-edge of the whorl wall marking the limit of its scar. In thick specimens of *N. dubia* (fig. 3), in *N. smithii*, Gray, and in *N. bicolor*, Récl. (figs. 4 and 4 *a*), there is a further thickening of the shelly deposit, which begins to spread over the remaining portion of the parietal wall in the direction of the apex. The columella-edge is additionally strengthened in *N. virginea*, Lamk., and the paries nearly concealed by the increased deposition; whilst in *N. intermedia*, Sow., and *N. punctulata*, Lamk. (figs. 5 and 5 *a*), this shelly deposit completely covers the parietal wall, stretches out from the columella-edge, and forms a veritable septum reaching one third of the way across the whorl, its free margin becoming thickened, pillar like, and firmly attached to the outer walls of the shell by its spreading ends.

The next link in the series is supplied by that very peculiar species *N. latissima*, Brod. (fig. 6), in which the septum with its pillar-like margin stands away from the columella-edge, so that although united posteriorly the septum and the remaining portion of the paries project independently into the single chamber of the shell: the septum is now the myophore. *N. fluviatilis*, Linn. (fig. 7), and an undetermined species (fig. 8) closely allied to *N. canalis*, exhibit a further stage in which these two partitions stand slightly apart; and the distance between them is successively increased in *N. canalis*, Sow. (fig. 9), *N. granosa*, Sow. (fig. 10), and *N. tahitiensis*, Lesson. The parietal wall in adult specimens of the last-named disappears entirely: it also is completely removed in *N. crepidularia*, Lamk. (fig. 11). The Eocene form *Tomostoma neritoides*, Desh. (fig. 12), undoubtedly comes very close to the last-named; not only does it resemble it in its external characteristics, but also in the internal arrangement of the septum and the lack of all trace of the parietal wall.

One or two other points about the septum are worthy of note.

Where the free edge is thickened and pillar-like, as in *N. intermedia*, *N. punctulata*, *N. fluviatilis*, and, to a lesser degree, in *N. latissima*, the angle it makes with the septiform columellar lip approaches the perpendicular; where, however, the septum is widely separated from the paries, as in *N. canalis* and the species that follow in the series quoted above, its free edge is thin, sharp, and inclined more out of the perpendicular, the whole septum sloping back from the aperture.

Towards the middle in *N. canalis* the free edge of the septum has a somewhat acuminate projection corresponding to that noted above on the columella-edge in *N. cornea*, &c.

Viewed through the aperture of the shell only a very small portion of the septum can in these latter cases be seen; in its earlier stages in the other species cited it is of course quite out of sight. The shifting of the septum away from the parietal wall is due to a purely mechanical cause. Just in proportion as the whorls of the shell increase more rapidly and the spire at the same time becomes more depressed, so the latter approximates the posterior angle of the aperture, and consequently the inner wall of the last whorl becomes smaller and smaller and less and less adapted to serve as a myophore. Moreover, as the shell becomes flattened and the septiform columellar lip extends further and further outwards from the axis, the angle at which the retractor muscle would have to act in order to withdraw the extended animal, were its fixed point still the remnant of the paries, would be one of great disadvantage from a mechanical point of view, and hence a fresh attachment, as near to and as much above the aperture as possible, becomes of great importance and is obtained by the forward movement of the septum already described. The manner of this forward growth will be best dealt with later on when the growth of the shell of *Velates conoideus* is under consideration.

In all cases, too, the scars of the anterior and posterior retractor muscles are pronounced in proportion to the strength of the muscles that were attached thereto, and, in consequence, to the thickness of the shell and the septum. It must also be borne in mind that the flattened columellar lip characteristic of *Neritina* and *Nerita* is formed by the callus, as likewise is the "shelf" in *Septaria* [= *Navicella*].

In *Nerita* the myophore at first sight appears as if it were a remnant of the paries; but a closer inspection, if one may judge from such typical forms as *N. peloronta*, Linn. (fig. 14), *N. polita*, Linn., and *N. plexa*, Chemn., reveals the fact that it is merely the septum, all trace of the inner walls and columella having been removed.

Velates, so far as at present known, is represented by but two species—*V. conoideus*, Lamk., and *V. equinus*, Bez., which occur together in the Lower and Middle Eocene of the Paris Basin. The shell of the latter attains to close upon 4 whorls when full-grown, and at that age corresponds in size with specimens of *V. conoideus* that have only completed about 3 whorls. The internal construction of the two at these respective periods is so similar that the description of one of them is sufficient, and no further reference need be made to the growth of the shell in *V. equinus* since it is perfectly normal. During the early stages of its growth, *i. e.* up to about 3 or $3\frac{1}{2}$ whorls, the myophore in the young *Velates* shell (fig. 16) is formed of the remnant of the parietal wall strengthened by shelly deposit much in the same way and degree as it is in *Neritina virginea.* No trace of a prominence is perceptible at first on the thin and sharp columella-edge, but by the time $3\frac{1}{2}$ whorls are finished it is plainly discernible, and with the completion of the fourth whorl it attains its maximum development (fig. 17 *d*). The angle the columella-edge makes with the columellar lip scarcely if at all exceeds 45° and is less in the earlier stages, whilst the whole myophore rakes back from the aperture and is not visible from without. After the completion of the fourth whorl the growth of the septum is comparatively rapid and increase takes place especially along that portion of its free margin which is furthest from the callus. By the time $4\frac{1}{4}$ whorls are complete the free margin is almost perpendicular to the callus and has become thickened and pillar-like, a slight fold on it marking the position of the late prominence (fig. 18 *d*). The appearance of the septum at this stage is most like that of *Neritina punctulata* amongst recent species. Shortly after the completion of $4\frac{1}{2}$ whorls (fig. 20 *d*) the septum alone constitutes the myophore, the columella and paries having been absorbed, and occupies the relative position it retains throughout the remaining period of growth: its free and thickened edge is quite perpendicular to the callus, and the greater portion becomes visible through the aperture, although the whole septum curves inwards as it projects into the chamber of the shell. So far, therefore, as the myophore is concerned the shell of *Velates conoideus* offers in the growth of the individual a series of conditions which in the recent forms find their parallel in distinct species:—in its earlier stages the paries and the incipient septum go to form the myophore, as in the instances quoted; in the later period the septum alone plays that part, as in *Neritina crepidularia.*

The scars of the retractor muscles, both anterior and posterior, become more marked as the individual grows, the former especially deepening with age, and there is a well-marked anterior palatal apophysis which gradually becomes fainter as the shell grows and finally almost entirely disappears. The callus which in the young shell does not extend very far over the adjacent portion of the body-whorl (fig. 15) gradually spreads further and further (figs. 16, 17), till by the time $4\frac{1}{4}$ whorls have been completed (fig. 18) it has covered nearly one half of the body-whorl and its line of demarcation is in one plane with that of the margin of the outer lip. The rate of increase of the third and following whorl is, moreover, proportionately greater than that of the preceding ones.

It is at this point that the great change in the manner of growth of the shell begins. First of all the callus is greatly thickened till it becomes in proportion to the shell itself larger and thicker than at any subsequent period (fig. 19). In the next place, further increase of the shell begins to be effected by the addition of fresh material not merely to the outer lip and columella alone as in normal growth, but all the way round in the plane of the outer lip, as first evinced by the deposition of periostracal layer along and over the outer margin of the enlarged callus (fig. 20), the lines of deposition, or growth, being continuous with those of the outer lip. In other words, were it not for the overlap of the callus the peristome would be complete, as in *Neritina crepidularia* and *Tomostoma neritoides*. Deposition also takes place over the whole surface of the callus. The direction of growth is in this manner completely changed. Instead of developing spirally, round an axis of which the protoconch forms the apex, the shell enlarges radially, the new axis being the pillar-like margin of the septum and its apex the point, on the exterior of the body-whorl, situated immediately over the junction of these two. In this new condition of affairs the callus, which is at right angles to the new axis, lies of course completely athwart the direction of growth and decidedly in the way of further extension, so that the animal must have found itself much in the same predicament that a limpet would do were it to be suddenly half-decked when its period of growth was still far from complete.

A grave problem in its domestic architecture was thus raised, and the solution forms the most interesting feature in the life-history of this species; for layer by layer, as deposition of fresh shelly matter took place without, a corresponding amount of material was removed on the inner side of the callus, and the additional room required thus obtained. Put in homely phraseology, this mode of enlarging a tenement reminds one of nothing so much as of the Irishman, who raised his roof by digging out the floor of his cabin.

The ultimate outcome of this novel mode of increase is that, in the adult *Velates*, that portion of the shell included between the margin of the outer lip and a line (A B, fig. 21) joining its extremities and passing round and a little below the apex on the further side is normal, whereas the remainder is formed out of callus past and present. This comes out very clearly in the various sections of the shell presently to be described. Of course the walls around the apex which require to be thickened as the shell increases in size, to make them as durable as the rest, are strengthened in the usual way by the deposition of fresh shelly matter within, so that, in an old shell, what was once the cavity inhabited by the young animal has become solid shell.

The changes which take place in the external form of the test of *Velates*, as was to be expected, find their reflection in the intimate structure of the shell itself. An axial section whose plane passes close to and almost parallel with the edge of the columellar lip, but just misses the apex itself, has been made in each of three young shells of different ages, and the sections stained with picro-carmine to bring out the structure more clearly. In the first, a specimen of about 3 whorls (Plate XXXII. fig. 22 *a*), the shell-wall near the apex shows three readily distinguishable layers:—the outermost, or periostracal layer, the crystalline, and the innermost layer, which in this case consists of the material laid down not merely as a lining to the shell, but to fill up the space no longer occupied by the animal and to thicken the shell where, having been formed when the animal was young, it was too thin for the present requirement of its occupant.

The periostracal layer, which shows a tendency to divide into two zones (fig. 22 *b*), is translucent and presents to the eye a fibrous structure, the fibres being arranged at right angles to the surface in the region of the apex; but as the layer is followed down towards the anterior end of the columellar lip they change their direction gradually till they assume the feather-like appearance familiar in shell-structure and are arranged in a direction approximately parallel with the layer itself (fig. 22 *c*).

The second principal layer also exhibits a fibrous appearance consequent on the arrangement of its crystalline plates, which near the apex are nearly but not quite at right angles to the surface. As the columellar lip is approached these become more inclined, till on joining those of the columellar lip itself they unite with them and sweep through an arc of more than a quarter of a circle (fig. 24 *c*).

The layers of growth can in places be clearly seen (figs. 22 *a*, *b*). The innermost deposit is confined to the neighbourhood of the apex and thins out as it recedes therefrom: it shows in section the cross-hatched structure so common in sections of shell and due to the especial arrangement of its component plates.

That the myophore at this stage is still formed in its upper part of the parietal wall is evident from its structure and its continuity with the outer wall next the apex (fig. 22 *a*). The middle portion of the myophore and the posterior wall have unfortunately been broken away in grinding this section. Nevertheless sufficient of the base of the former and of the callus out of which that base has been formed is left to show that even at this early age a considerable enlargement of the interior by absorption has taken place.

In the next older specimen, one of about three and a half whorls (fig. 23 *a*), the remnant of the parietal wall can be traced, the section being perfect, for quite two-thirds of the length of the myophore, whilst in the outer wall on the posterior side of the section the remnant of another original wall is present. A portion of the periostracal layer, about halfway down that side, curves inwards, traverses the shell-wall, and abruptly terminates on the inner side ($p'.l'.$): it is overlain by the edge of the callus which comes up to this point and which is in its turn covered by a fresh deposit of periostracal layer that joins on to the first one. This junction is not a true suture, since it does not mark the union of two whorls. The extent to which the callus has been absorbed on its inner side is clearly shown, as also the vertical arrangement of its component plates. This structure, however, is still better seen in more advanced stages of growth.

The third section (fig. 24 *a*) has been taken of the young shell at the stage when its four and a half whorls have been completed and the period of radial growth entered on, just at the time when the callus having attained its maximum development begins to be covered all round its margin by the periostracal layer. The myophore is still in part formed of an old outer wall of the test, but that portion was callus (c'), as shown by the structure, and has been shaped to suit its present position, as the transverse direction of its lines of growth testify. The wall on the posterior side of the section is built up of an old whorl, of callus, and of infilling material. The absolute apex of each of these two last specimens appears in the succeeding section of the respective shells, and here may be seen the remains of the true spire, such as it is, and the overlapping sutures (fig. 24 *b*).

These remnants exist in the adult shell, unless indeed it be a worn specimen; all other traces of former walls have disappeared. A section taken through a full-grown specimen as nearly as possible in the plane of the septum (fig. 25), and stained with picro-carmine, clearly reveals the intimate relationship between the myophore and the neighbouring walls of the test and demonstrates beyond doubt the way in which they have been carved out of successive layers of callus, for the lines of growth can be traced right across the septum to its inner margin and reappear in the wall of the shell on the opposite side of the cavity (see also fig. 26). They may also be distinctly seen running round the walls on the interior surface of the shell[1].

The composition and intimate microscopical structure of the *Velates* shell likewise call for some remark, since further points of interest are presented by them.

The term *periostracal layer* has been employed throughout, instead of *periostracum*, for the external layer, the reason being that it differs so widely in its composition from the chitinous substance which coats most shells, and which usually is known by the latter term, that its application in this instance might have been misleading.

This layer is remarkably hard and extremely difficult to cut through; it does not stain like the rest of the shell, but remains translucent with a cloudy fibrous appearance when seen in the microsections already described. It retains probably to a very high degree (especially in the young shell) the coloration and mottled markings which adorned the shell when living. Its line of junction with the underlying crystalline layer in the young shell and that portion of the adult where the growth is normal is even; but where it overlies callus the several layers of the two inosculate and the line of junction is extremely ragged and irregular (figs. 24 and 27). In the one case the mantle-edge that secreted it was advancing over a given area followed in regular order by the portion that furnished the material for the second layer; in the other the mantle was retreating from the area of deposition as the shell increased in size and so gave rise to overlapping of the two series of deposits, the irregularities that thus arose being further complicated by the fluctuations in the growth of the animal and its shell.

Under the delusion that this periostracal layer might, like the molluscan radula, prove to be very dense chitine, a portion was placed in Mr. G. T. Prior's hands for examination. He most kindly made a careful investigation of it, with the result that it

[1] These lines of growth were noted by Schmidel.

appears in the main to consist of calcic carbonate, since it dissolves with effervescence in dilute hydrochloric acid, leaving, however, an appreciable residue. This residue subjected to the usual tests, both with acids and under the blowpipe, proved to consist of silica, having a specific gravity which is nearer that of the crystalline than the amorphous state. Naturally it was at first thought that this silica might be a product of fossilization, but since the callus, which was equally exposed to the same influence, yields no appreciable residue, this does not appear to be a tenable supposition; at the same time without further and more extended inquiries one hardly likes to look upon it as an original product of the animal[1].

The crystalline layer which forms the principal thickness of the shell-wall is composed of a single stratum of laminæ, the component fibres of which in each successive lamina run in a reverse direction to those of the preceding one, as originally described by Count Bournon[2] and subsequently by all writers on molluscan shell-structure.

The direction these plates take, however, in the present example is peculiar. In that part where the growth is normal (see fig. 21) their direction coincides with that of the lines of growth, their planes being perpendicular to the outer surface of the shell, just as seemingly obtains in an ordinary *Neritina* (e. g. *N. gagates*). In the remaining portion of the shell-wall beneath the periostracal layer the plates follow the curve of the shell, their planes radiating from the new apex and consequently being approximately parallel with the outer surface—approximately, because the sections show that in each major group of layers they 'feather' somewhat (figs. 25, 26, 27).

These walls being, as already mentioned, hewn out of successive margins of former callus, it follows naturally that in the outer margin of the callus itself the plates follow the same course—that is to say, are disposed in a crescent, at the extremities of which, their planes of inclination twisting to suit, they unite with those of the outer lip to form a continuous circle. Along the dentate columellar lip they also run parallel with the margin, and here, as elsewhere over the callus, their planes are at right angles to the exterior surface.

On reaching the posterior angle of the aperture this series of lamellæ (viewed from the exterior) abruptly bifurcates, one set curving sharply towards the outer lip, the other in the opposite direction, and both commingling with, and becoming lost in, the marginal plates; the point of junction of the two series thus forms a centre whence they stream off in three directions (fig. 28).

At the anterior angle the whole series curves towards the outer lip, becoming lost, as before, in the marginal set. Across the central portion of the callus they run in an oblique direction, radiating from

[1] Schmidel noted that this layer did not appear to be entirely composed of lime.

[2] 'Traité complet de la Chaux carbonatée,' etc. tom. i. (1808) p. 310. See also Gray (J. E.), Phil. Trans. cxxiv. (1833) p. 789; Bowerbank (J. S.), Trans. Micro. Soc. i. (1844) p. 128, pl. xv. fig. 1; and Rose (G.), Abhandl. k. Akad. Wissensch. Berlin, 1858 (1859), p. 89. pl. iii.

a point situated a little way in from the posterior angle, their course as they approach the margin becoming uniformly deflected to the left, *i. e.* in the direction of the anterior angle of the aperture. The nature of this arrangement is, however, more easily gathered from the figure than realized from a mere description. Seen from the inner aspect the relationship of the internal septum to this structure becomes apparent (fig. 29). The point by the posterior angle of the aperture whence the plates radiate in three directions marks the junction of the septum with the outer wall; the centre of radiation a little further in falls just beside the septum in the middle of its curved inner side, so that the direction of the plates in the septum itself very nearly corresponds with the curvature of its walls, or, to put it in another way, the 'graining' of the septum is but slightly 'on the cross.' The whole system of construction of the callus, therefore, would appear to foreshadow the future requirements of the animal, and its component plates to be so arranged that when by erosion in the course of growth its unabsorbed portions form part and parcel of the walls and septum of the shell these plates shall be in the right position to impart the greatest strength and durability to the whole that is possible under the circumstances, for the lines of growth in the callus-formed portion are of necessity lines of weakness.

Mr. H. A. Miers was so good as to investigate a portion of the crystalline layer from the callus, testing its specific gravity by means of density fluids. It floated in a liquid in which aragonite and tourmaline sank; but foundered in one which would support beryl and calcite. On account of its porous nature, the observed specific gravity of the material must in reality be too low and the crystalline callus is therefore more likely to be aragonite than calcite.

Mr. Miers further reports :—"By taking some of the very finest powder and examining it with a twelfth oil immersion, I am able to find some specks which are undoubtedly calcite (by cleavage and opt. char.). In section it is impossible to determine the substance—because the use of the same objective with polarized light shows that it consists of very minute overlapping fibres even where it appears homogeneous under the quarter. Some of the powder looks to me more like aragonite—little ragged fibres with straight extinction, no cleavage, and the double refraction of aragonite.

"The final result is then—an extremely fine fibrous structure; the presence of calcite proved; the presence of aragonite highly probable."

The manner in which the myophore and the callus shift forward with the growth of the shell in *Neritina* can now be readily understood. Fresh shelly matter is added to the outer and a corresponding quantity removed from the inner side. No section can well be taken to prove this to demonstration in the majority of the species of the genus, but in *N. crepidularia* it can be shown that the callus does thus change its position and move through a segment of a circle, keeping pace in this way with the growth of the rest of the shell (fig. 30); and the same is true of *Septaria* [=*Navicella*]. In